Climatic effects on woody plant density and diversity in tropical montane treefall gaps

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Abstract: Disturbances caused by treefalls are thought to be crucial for maintaining tree species diversity in tropical forests. However, relatively little is known about the influence of abiotic factors other than light on the diversity of woody plants in treefall gaps. In the Monteverde cloud forest, temperature, nutrients, and cloud cover all differ between the Pacific slope and the ridge top. We hypothesized that these differences between the Pacific slope and the ridge top would influence species density and diversity of woody plants in treefall gaps. Density and diversity of morphospecies was high in Pacific slope gaps compared to ridge gaps. However, the relationship between number of individuals and number of species was very similar between habitats (≈ 1 species added per 2.4 individuals in both habitats). Apparently reduced primary productivity at high elevations leads to a reduced number of tree individuals per unit area, which leads to reduced species richness and diversity. There was little overlap of morphospecies between gaps within either habitat (only 0.9% of morphospecies were found in more than one gap). It appears that abiotic factors can predict broad patterns of woody plant density and diversity of treefall gaps in tropical cloud forests, but cannot easily predict the species composition of any particular gap.

Key Words: Costa Rica, cloud forest, forest dynamics, Monteverde, saplings, seedlings, succession

Introduction

Treefall gaps are important to the regeneration and turnover of species in tropical forests because they produce diverse light conditions that permit the establishment of many tree species (Connell 1978, Denslow 1987). Brokaw (1985) suggested that gaps are centers of high species richness because they create areas of high light availability in the forest. Thus gaps sustain both species that require high light and those that occur in the low light conditions of mature forest understories. Brady and Wray (1995) found that the broad variability in microhabitat conditions in and around gaps contributes to higher species diversity in woody plants. They also found very little overlap of morphospecies between individual gaps. Although the light gradient in treefall gaps is clearly important for tree diversity, relatively little is known about how other abiotic factors such as temperature and soil nutrients, and water availability influence the plant communities that colonize treefall gaps. This study compared the density and diversity of plant communities colonizing treefall gaps in two elevation zones of the Monteverde cloud forest that differ in temperature, precipitation, and soil characteristics.

The Monteverde cloud forest, which straddles the continental divide of the Cordillera de Tilarán, sustains large microclimatic differences over a short altitudinal range. Due to northeasterly tradewinds, cloud forest microclimates vary dramatically with elevation and annual rainfall. The elfin forest along the ridge of the divide (1700 - 1800 m asl) experiences more extreme windstorms, has cooler temperatures and probably has lower nutrient availability in the soil than the lower Pacific slope (1500 - 1600 m asl; Haber 1996). The density and diversity of saplings was higher in treefall gaps on slopes than ridges in the

Atlantic lowland forests of Costa Rica (La Selva Biological Station; Denslow 1995), which suggests that abiotic factors other than light may influence the density and diversity of woody plants in treefall gaps that occur on ridges. Low temperatures at higher elevations (e.g., on mountain ridges) tend to reduce mineralization rates and therefore the soil in these enviroments is relatively nutrient-poor. Low nutrient availability may limit primary productivity and therefore the number of plants per unit area that colonize treefall gaps. If so, the diversity of treefall gap communities may be lower at high elevations than mid elevations by virtue of having fewer total individual plants in the community (Denslow 1995).

Methods

We selected three treefall gaps, of similar size (≈ 10 m in length) and age, on both the Pacific slope (1500 - 1600 m asl) and ridge top (1750 - 1800 m asl) along the trails near the Monteverde Biological Station. We defined gaps as disturbed areas in the forest where an adult canopy tree had fallen, producing an area free of canopy cover. We sampled two transects in each gap, one 7-m transect parallel to the slope and another 2-m transect perpendicular to the slope from the center point of the gap. We collected leaves from all free-standing woody plants < 2 m tall within a 1 m swath running the length of our transects. Leaves were subsequently sorted into morphospecies in the laboratory (Brady and Wray 1995). For each gap, we calculated the density of each morphospecies, species richness, and the Shannon-Weiner diversity index. Then we compared the density, diversity, rank abundance curves, species addition rates (the number of species accumulated per individual sampled), and the proportion of unique species for both the Pacific slope and ridge top gaps.

Results

Our transects included a total of 200 individuals representing 80 morphospecies of woody plants. The mean density (± 1 SD) of woody plants was greater in Pacific slope gaps (5.8 ± 1.3 plants/m^2) than in ridge gaps (1.6 ± 1.9 plants/m^2; $t = 3.18$, $df = 4$, $p = 0.03$). Pacific Slope gaps also had many more total morphospecies than ridge top gaps (65 vs. 17 respectively). There were 63 morphospecies unique to the Pacific slope and 15 unique to the ridge. Two morphospecies were found in both Pacific slope and ridge gaps. The relationship between density and diversity was similar between the Pacific slope and ridge gaps in that morphospecies per individual did not differ between the two elevations: 65 morphospecies per 156 individuals (0.42) on the Pacific slope and 17 morphospecies per 44 individuals (0.39) on the ridge (chi-square = 0.03, $df = 1$, $p = 0.85$). There was a strong positive relationship across gaps between density and number of morphospecies and the same linear function can describe gaps at both elevations (species richness = 1.26 + 3.71•density; $r^2 = 0.89$, $df = 1$, $p = 0.004$; Fig. 1).

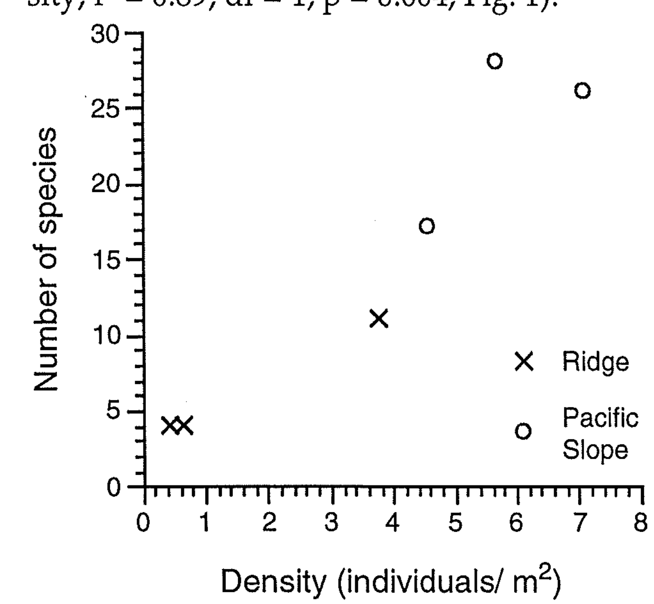

Figure 1. The relationship between density of woody plants and total number of morphospecies in gaps on the Pacific slope and near the ridge top.

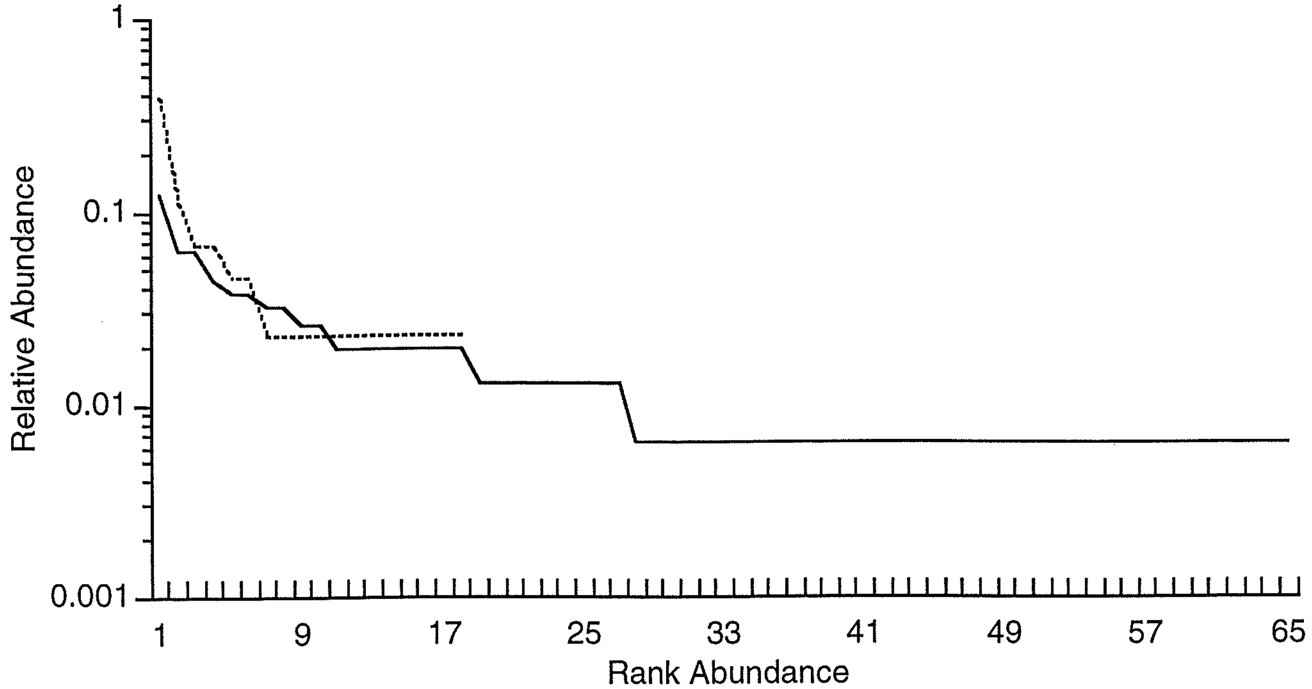

Figure 2. Ranked abundance of woody plant morphospecies in treefall gaps from two elevation zones of the Monteverde cloud forest, Costa Rica.

The proportion of morphospecies that occurred in only one gap was very high at both elevations: 62 of 65 (0.95) on the Pacific slope and 15 of 17 (0.72) on the ridge ($G = 3.16$, $df = 1$, $p = 0.09$). Species evenness (J) of the Pacific slope was similar to ridge gaps (mean ± SE = 0.90 ± 0.05 vs. 0.88 ± 0.07, respectively; $t = 0.21$, $df = 4$, $p = 0.85$), and was reflected in the similar shapes of the rank abundance curves (Fig. 2). The Shannon-Weiner diversity index (H′) of the Pacific slope gaps was greater than the ridge gaps (mean ± SE = 2.82 ± 0.17 vs. 1.48 ± 0.17, respectively; $t = 5.55$, $df = 4$, $p = 0.005$).

Discussion

The density and diversity of woody species in treefall gaps was greater on the Pacific slope than the ridge. This supports the hypothesis that abiotic differences associated with the two elevation zones can influence the community composition of woody species in treefall gaps. The abiotic factors that seem important in this case are cooler temperatures and lower nutrient and light availability on the ridge. Although we did not empirically measure the nutrient content of the soil on the ridge and on the Pacific slope, the soil on the ridge is likely to have lower nutrients because cooler temperatures decrease mineralization rates. Lower nutrient availability and productivity on the ridge may limit the number of individuals per unit area that the environment can maintain. Also, increased cloud cover at high elevations would decrease the light availability in gaps, which may further limit plant densities. Species accumulation rates (morphospecies per individual) were very similar between the two elevation zones (Figs. 1 – 2), which implies that abiotic factors that limit the density of woody plants may be adequate to explain lower species richness in ridge gaps (Denslow 1995).

One caveat is that low density of woody plants in gaps on the ridge may have been partly due to a higher abundance of herbaceous plants compared to the Pacific slope.

So it is possible that woody species in the ridge gaps may have to compete more intensely with herbaceous plants for light and nutrients. Brokaw (1983; cited in Denslow 1987) showed that shade cast by large-leafed herbaceous species (e.g., Araceae and Heliconiaceae) can reduce the abundance and distribution of tree seedlings. Further study is necessary to test whether competition from herbaceous plants influences the diversity of woody plants in gaps.

If abiotic factors completely determined woody species assemblages in treefall gaps, and abiotic conditions are as similar as they appear among gaps within elevation zones, morphospecies particular to either Pacific slope or ridge gaps should occur within virtually all gaps in their elevation zone. However, we found almost no overlap of morphospecies between gaps. This suggests that the species composition of individual gaps is also influenced by the proximity of adults to the gap and/or by seed dispersal mechanisms. If so, we probably need to combine spatially explicit models with a better understanding of plant life histories and dispersal biology to predict the species composition in treefall gaps.

Nonetheless, abiotic factors can apparently predict some broad patterns of density and diversity in the treefall gaps of tropical cloud forests. Because virtually every point within tropical cloud forests have been part of a treefall gap within the lifespan of canopy trees, understanding the factors that influence gap colonization by saplings is critical to our understanding of diversity within the forest as a whole.

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